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NEW SERIES, NO. 68

Studies on Skeleton Formation in Reptiles. III. Patterns of Ossification in the Skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata)

Olivier Rieppel

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Murra, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Studies on Skeleton Formation in Reptiles.

III. Patterns of Ossification in the Skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata)

Olivier Rieppel

Abstract

Patterns and sequences of ossification are described for the skeleton of the lizard *Lacerta vivipara*. Ossification processes follow regular patterns that may differ from patterns of chondrification of cartilaginous precursors. Problems of homology, relating to limb morphology, are discussed in detail, particularly the homology of the radiale and of the intermedium, which both fail the test of conjunction, and purported homologies of epiphyseal ossification centers as they relate to the interpretation of metacarpal I, the astragalus, and the hooked fifth metatarsal. Comparison with squamates showing limb reduction indicates that two types of skeletal reductions have to be distinguished: reduction due to failure of morphogenesis (chondrification), and reduction due to failure of ossification. This distinction is important in the interpretation of fossil skeletons subject to reduction, since the patterns of ossification may differ from those of chondrification.

Introduction

The study of the development of the reptile skeleton has resulted in a vast body of literature going back to the 19th century. However, most embryological work, if not a morphological description of early stages of morphogenesis, has tended to identify the origin of particular structures in ever earlier stages, and/or to address the underlying mechanisms of pattern formation at a molecular level. This is not the approach pursued in the present investigation. While chondrogenesis of many parts of the reptile skeleton is relatively well understood, little is known about ossification beyond circumstantial evidence that there may be some regularity to the patterns of ossification in different taxa, which furthermore may differ from patterns of chondrification.

Ossification following chondrification represents a special case of "ontogenetic repatterning" (of a different meaning as that implied by Wake & Roth, 1989). Ossification processes may produce a mismatch of numbers and topological correspondence of cartilaginous and bony parts, as

the structural pattern of cartilaginous precursors is replaced by a new pattern of bony elements. Issues relevant in this context and discussed in this paper are the following: the distinction of cartilage versus membrane bone (Patterson, 1977) and the serial homology of dorsal, sacral and caudal ribs; the homology of the reptilian radiale and astragalus (see also Rieppel, 1992c), as well as of the ossified intermedium of lizards in which it occurs; and problems of homology created by epiphyseal centers of ossification in manus and pes.

This contribution will focus on the pattern of ossification within the endoskeleton and the exoskeleton during late embryonic and postembryonic stages of the viviparous lizard *Lacerta vivipara*. Earlier findings (in the gekkonid lizard *Cyrtodactylus*: Rieppel, 1992b) indicated that ossification processes do, in fact, give rise to patterns that are different from those observed during chondrogenesis. Comparison of the results of this investigation with skeletal reductions observed in fossil and extant reptiles will allow a test of the assumption that patterns of reduction provide a mirror image of patterns of morphogenesis. If pat-

terms of chondrification versus ossification indeed represent two different classes of phenomena, each regular within itself, then two meanings of skeletal reduction emerge. The first mode of reduction will mirror the failure of a given element to form, i.e., to become preformed in cartilage; the other mode of reduction will refer to the failure of an element, once formed, to ossify. The difference between these two aspects of reduction should correlate with the degree to which ossification patterns replace chondrification patterns. The distinction of two modes of skeletal reduction is of relevance in the interpretation of fossil material.

The extensive literature on the development of the reptile skull has been summarized by Bellairs and Kamal (1981). These authors note (p. 4) that "The development of the osteocranium has been less critically studied than that of the chondrocranium. . . . Still less is known about the important changes which occur in early postnatal life involving ossification and growth." More recent work, not cited in the review by Bellairs and Kamal, and including data on the development of the osteocranium in embryonic and postembryonic stages of squamates, includes studies of the lizards *Eumeces latiscutatus* (Hikida, 1978), *Podarcis muralis* (Rieppel, 1984), and *Podarcis sicula* (Rieppel, 1987b) and the snakes *Elaphe obsoleta* (Haluska & Alberch, 1983) and *Natrix natrix* (Rieppel, 1988), as well as a variety of boid snakes (Irish & Alberch, 1989; Irish, 1989). Ontogenetic data on skull development are also included in Gauthier et al. (1988a,b).

The postcranial axial skeleton of reptiles has been reviewed by Hoffstetter and Gasc (1969). More recent contributions dealing with the ontogeny of the lepidosaurian vertebral column are those of Winchester and Bellairs (1977) and Borchwart (1977). Studies on the development of the tetrapod limb abound, and no attempt is made here to present a complete review of the literature. Classic papers on the subject are those of Holmgren (1933) and Schaeffer (1941). More recent general reviews include Hinchliffe and Griffiths (1983), Goodwin and Trainor (1983), Shubin and Alberch (1986), and Horder (1989). Work on the development of the squamate limb and limb rudimentation (Sewertzoff, 1908, 1931) is summarized in Raynaud (1985). The most recent comprehensive accounts of limb development in reptiles are the following: for a lizard, Mathur and Goel (1976: *Calotes*); for a crocodile, Müller and Alberch (1990: *Alligator*); and for a turtle, Burke and Alberch (1985: *Chelydra*). Of all these contributions, only Mathur and

Goel (1976) offer details on the sequence of ossification of the limb elements.

Materials and Methods

This study is based on cleared and stained late embryonic and postembryonic developmental stages of *Lacerta vivipara*. Cartilage was stained with Alcian blue, bone with alizarine red (Dingerkus & Uhler, 1977); the procedure of clearing and staining followed Potthoff (1984).

The material investigated includes 8 embryos and 15 postembryonic stages. Where possible, snout-vent length (SVL) was measured before clearing and staining to an accuracy of 0.5 mm; in some specimens, SVL had to be measured, as accurately as possible, on cleared and stained specimens (SVL*). Inaccuracies in the determination of body size do not affect conclusions related to patterns of ossification because, although these patterns were found to be highly consistent, the degree of ossification is not closely related to overall body size. A normal table of development, defining embryonic stages of *Lacerta vivipara*, was produced by Dufaure and Hubert (1961), but it could not be used in the present study because most of the embryonic material was obtained on loan after it had been cleared and stained.

Abbreviations for institutions are as follows: FMNH, Field Museum of Natural History, Chicago; MBS, Natural History Museum, Basel; MHNG, Muséum d'Histoire Naturelle, Geneva; NMBE, Natural History Museum, Berne; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; and UMMZ (UMFS), University of Michigan Museum of Zoology Field Series. Collection numbers and body size for the specimens investigated are as follows: FMNH 66933 (SVL = 20 mm, newborn); FMNH 78365 (SVL = 29 mm); MBS 4240 (SVL = 27.5 mm); MBS 5625 (SVL = 34 mm); MBS 5949 (SVL = 30 mm); MBS 11898 (SVL = 33.5 mm); MBS 14918 (SVL = 17.5 mm, immediate newborn); MBS 15949 (SVL = 27 mm); MBS 16487 (SVL = 33 mm); MHNG 806.53 (SVL = 31.5 mm); MHNG 806.58a (SVL* = 16.5 mm); MHNG 806.58b (SVL* = approx. 20.5 mm); NMBE 1'001'297 (SVL = 24.5 mm); NMBE 1'001'298 (SVL = 26.5 mm); NMBE 1'001'299 (SVL = 30 mm); UMMZ 189895 (SVL* = approx. 11 mm); UMMZ 189896 (SVL* = approx. 22 mm); UMMZ 189898 (SVL* = approx. 19 mm); UMMZ 189899 (SVL* = approx. 15 mm); UMMZ 189900

(SVL* = approx. 9 mm); UMMZ 189903 (SVL* not measurable); and UMMZ 189906 (SVL* = approx. 7 mm). Collector's note identifies MBS 14918 as an immediate newborn specimen out of a litter constituting the series MBS 14918–14922.

The lacertid material studied was compared with the material of the gekkonid lizard *Cyrtodactylus* described by Rieppel (1992b), as well as with a number of cleared and stained developmental stages of *Sphenomorphus indicus* (Scincidae), all embryos removed from UMMZ 190346; UMMZ 190422 (SVL* = 21 mm), UMMZ 190423 (SVL* = 22 mm), UMMZ 190424 (SVL* = 22 mm), UMMZ 190425 (SVL* = 22 mm), UMMZ 190426 (SVL* = 23 mm), UMMZ 190535 (SVL* = 20.5 mm), and UMMZ 190536 (SVL* = 24 mm). Reference will also be made to a series of cleared and stained specimens of *Draco melanopogon* (Agamidae), including FMNH 144733 (SVL = 35 mm), FMNH 149980 (SVL = 40.5 mm), FMNH 150015 (SVL = 37 mm), FMNH 150021 (SVL = 46 mm), FMNH 150048 (SVL = 42 mm), FMNH 150066 (SVL = 50 mm), and FMNH 221025 (SVL = 30.5 mm).

The ossification process of the fifth metatarsal bone was compared to cleared and stained specimens of two iguanid taxa, *Urosaurus ornatus* and *Calotes versicolor*. Specimen numbers are as follows: *Urosaurus ornatus* UMMZ(UMFS) 03279, 16-day-old embryo; UMMZ(UMFS) 03281, 29 days old; UMMZ(UMFS) 03282, 31 days old; UMMZ(UMFS) 03283, 34 days old; UMMZ(UMFS) 03284, 40 days old; and UMMZ(UMFS) 03285, newborn stage. Critical stages of *Calotes versicolor* are FMNH 180503 (SVL = 54.5 mm); FMNH 180522 (SVL = 22.5 mm); FMNH 180608 (SVL = 23 mm); and FMNH 180634 (SVL = 42.0 mm).

Morphological Description

The material studied allows the determination of ossification sequences in the postcranial skeleton with a high degree of resolution. Resolution is less complete for the sequence of ossification of skull bones. Additional embryological material and histological techniques are required to determine whether cranial bones, which appear to start ossification simultaneously in the available material, do in fact ossify sequentially. The original plan to present the patterns of ossification for the whole skeleton arranged in a sequence of developmental stages had to be abandoned, because (a) the overall degree of ossification shows no close correlation

with absolute body size, and (b) there is intraspecific variation in the detailed timing of the onset of ossification in various skeletal components. For example, the interclavicle and scapula start ossification after the clavicle in UMMZ 189900 at a stage when the braincase or the splanchnocranium has only just started to ossify; in MHNG 806.58a, however, the exoccipitals are in an advanced stage of ossification, and replacement bone has started to develop in the basioccipital, basisphenoid, quadrate, epipterygoid, and ceratobranchial I, whereas the clavicles are still the only elements of the pectoral girdle that have begun to ossify. Changes of timing of ossification affect skeleton compartments relative to one another, but not the sequence of ossification within these skeletal compartments. The patterns of ossification will therefore be discussed separately for the various skeletal components: the skull, vertebral column, pectoral girdle, pelvic girdle, forelimb, and hind limb (table 1).

General Remarks

Broad trends in the ossification of the skeleton of *Lacerta vivipara* (and other squamates investigated) can be summarized in terms of very general patterns. A pronounced anteroposterior gradient dominates ossification of the axial skeleton. The first ossification appears in the skull; the vertebrae, as well as the associated ribs and haemal arches, follow in an anteroposterior sequence. This gradient does not determine ossification sequence within the skull, however, except for the skull roof, which closes in an anteroposterior sequence.

The onset of ossification of the dermal pectoral girdle (clavicles) precedes ossification in the chondral elements of the pectoral girdle or in the pelvic girdle, but ossification of the chondral pectoral girdle lags somewhat behind ossification of the pelvic girdle. Stylopodial (humerus/femur) and zeugopodial (radius-ulna/tibia-fibula) elements of the forelimb and hind limb ossify more or less simultaneously, whereas ossification of autopodial (particularly tarsal) elements of the hind limb precedes ossification of equivalent (especially carpal) elements in the forelimb.

Axial Skeleton

THE SKULL—The first elements to ossify in the skeleton of *Lacerta vivipara* (as seen in UMMZ

TABLE 1. The onset of ossification in the skeletal elements of *Lacerta vivipara*. + indicates the initial stages of ossification; +/0 indicates initial perichondral ossification in endochondral elements.

embryonic (prenatal) stages	dermatocranium	neurocranium	splanchnocranium	postcranial axial skel.	clavicles	interclavicles	scapula	coracoid	ilium	pubis	ischium	humerus	radius/ulna	femur	tibia/fibula
UMMZ 189903	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
UMMZ 189906; 7mm	+	+	+	0	+	0	0	0	0	0	0	+	+	+	+
UMMZ 189900; 9mm	+	+	+	+	+	+	+	0	+	+/0	0	+	+	+	+
UMMZ 189895; 11mm	+	+	+	+	+	+	+	0	+	+	0	+	+	+	+
UMMZ 189899; 15mm	+	+	+	+	+	+	+/0	0	+	0	0	+	+	+	+
MHNG 806.58a; 16.5mm	+	+	+	+	+	0	0	0	+	+	0	+	+	+	+
UMMZ 189898; 19mm	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
MHNG 806.58b; 20.5mm	+	+	+	+	+	+	+	+/0	+	+	+	+	+	+	+

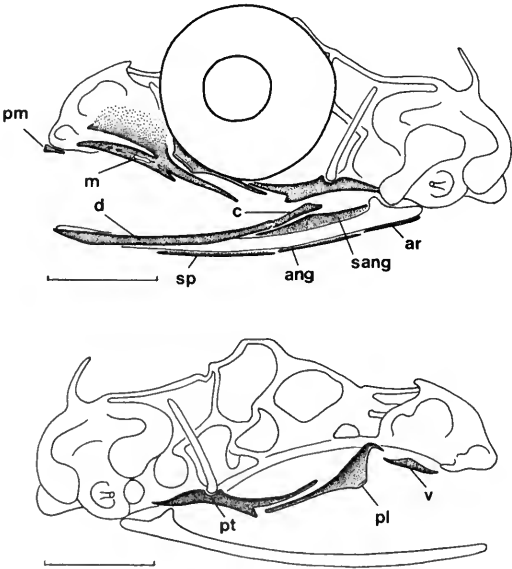


FIG. 1. **Top:** The dermatocranium of *Lacerta vivipara* (UMMZ 189903) in left lateral view. **Bottom:** Palatal ossifications of *Lacerta vivipara* (UMMZ 189903) in right lateral view. Scale bar = 1 mm. Abbreviations: ang, angular; ar, articular; c, coronoid; d, dentary; m, maxilla; pl, palatine; pm, premaxilla; pt, pterygoid; sang, surangular; sp, splenial; v, vomer. Stippling in this and all following figures indicates areas of ossification.

189903, fig. 1) are those of the upper jaw and bones related to the mandibular arch (see also Rieppel, 1987b). The premaxilla is a tiny splint of bone underlying the anterior tip of the nasal capsule; the maxillary is represented by loosely defined lacunae of mineralization lining the margin of the buccal cavity. The lateral aspect of the nasal capsule is covered by a sheet of faintly visible dermal ossification. No teeth have yet developed.

Elements associated with the mandibular arch are more clearly defined. The pterygoid is well advanced in ossification, which corresponds to earlier observations that the pterygoid bone is the first to ossify in the dermal plate (in *Podarcis sicula*: Rieppel, 1987b). It starts ossification in its middle portion, which underlies the processus ascendens of the palatoquadrate; in UMMZ 189903 it has already expanded backward to reach the quadrate, and it forms an elongated overlapping contact with the posterior process of the palatine. The palatine bone is well ossified along its medial margin and has developed a more weakly ossified lateral palatal shelf arching over the choanal tube. The vomer is represented by a small splint of ossification that underlies the nasal capsule without yet having established contacts with neighboring elements.

Dermal bones wrapping around Meckel's cartilage again are fairly advanced in ossification; earlier studies have shown the prearticular to be the first element to ossify (in *Podarcis sicula*: Rieppel, 1987b). In UMMZ 189903 all elements are identifiable, although the splenial and angular are still rather weakly ossified. Perichondral ossification has also begun around the posterior end of Meckel's cartilage, forming the retroarticular process. The ossification of the dentary is restricted to the lateral aspect of Meckel's cartilage.

The identification of the coronoid in this cleared and stained embryo presents some problems as compared to earlier studies based on serial sections stained after Bodian (of *Podarcis sicula*: Rieppel, 1987b). Histological investigations showed the coronoid bone to start ossification within the central tendon of the external adductor muscle independently from other jaw bones. In the cleared and stained specimen, the posterior end of the dentary is hardly distinguishable from a continuing ossification that rises into a rudimentary coronoid process and that will, in later stages, form the coronoid bone. This is one instance where the power of resolution of histological techniques proves superior to, or at least produces different results than, clearing and staining; a second example will be provided by the upper temporal arcade. Investigating the sequence of development of cranial bones in the anuran genus *Bombina*, Hanken and Hall (1988) noted that early foci of ossification may be visible in serial sections long before they show up in cleared and stained specimens.

In the next stage available (UMMZ 189906, SVL = 7 mm, fig. 2), the bones present in the previous stage have become more clearly defined, and other elements have been added. The tooth-bearing lower edge of the maxilla is more solidly ossified, and teeth have developed but are not yet ankylosed. The ascending process of the maxilla is only weakly ossified and, except for its posteriormost part, it appears to develop independently from the tooth-bearing edge of that bone. The jugal bone appears as an elongate and slightly curved splint of bone above the maxilla in a suborbital position. The prefrontal is represented by a triangular ossification in the anterodorsal corner of the orbit; it remains widely separated from the jugal. The nasal first appears as a thin and weakly ossified bone overlying the nasal capsule. The frontal bones are paired, each forming a slender and curved ossification mapping the dorsal margin of the orbit. The divergent and tapering posterior parts of the fron-

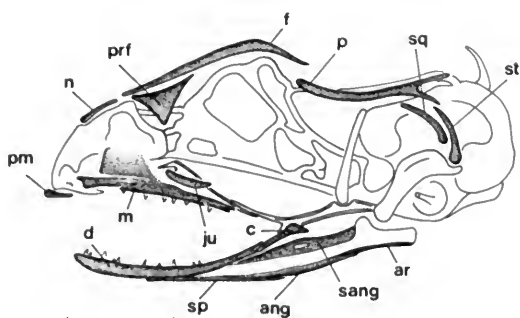


FIG. 2. The dermatocranium of *Lacerta vivipara* (UMMZ 189906, SVL* = 7 mm) in left lateral view. Scale bar = 1 mm. Abbreviations: ang, angular; ar, articular; c, coronoid; d, dentary; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; prf, prefrontal; sang, surangular; sp, splenial; sq, squamosal; st, supratemporal.

tals map the extent of the broad frontoparietal suture, which in squamates is broader than the nasofrontal suture (Estes et al., 1988).

The parietal bones are represented by narrow strips of ossification extending along the taenia marginalis. The degree of ossification of the bone differs on the two sides of the head of specimen UMMZ 189906. On the right side there is only a faint posterior bifurcation of the parietal ossification, while on the left side the parietal is represented by the characteristic triradiate ossification mapping its lateral and posterior margins and the supratemporal process. On both sides of the head, the supratemporal is represented by a curved ossification, tapering anteriorly and barely reaching the supratemporal process of the parietal ossification on the left side of the head, but articulating with the quadrate cartilage on the right side. The squamosal is still missing on the right side of the head, but it is present on the left side as a curved splint of ossification lying anterior and parallel to the supratemporal but not yet reaching back to the quadrate. The squamosal, therefore, appears to ossify after the supratemporal. The appearance of the squamosal at this stage of development indicates that the bone will continue to ossify (grow) in a caudorostral direction (see also Rieppel, 1984). These results differ from earlier observations based on serially sectioned material (of *Podarcis sicula*: Rieppel, 1987b) which indicated that the elements of the upper temporal arcade ossify almost simultaneously in a continuous strand of cell condensation.

In the lower jaw, the depth of the dentary ossification has increased. The coronoid bone is now

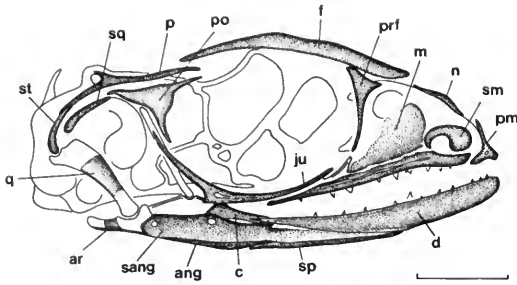


FIG. 3. The dermatocranium of *Lacerta vivipara* (UMMZ 189899, SVL* = 15 mm) in right lateral view. Scale bar = 1 mm. Abbreviations: ang, angular; ar, articular; c, coronoid; d, dentary; f, frontal; ju, jugal; m, maxilla; n, nasal; p, parietal; pm, premaxilla; po, postorbitofrontal; prf, prefrontal; q, quadrate; sang, surangular; sm, septomaxilla; sp, splenial; sq, squamosal; st, supratemporal.

more clearly identifiable, as are the splenial and angular.

Subsequent stages of embryonic development (UMMZ 189899, SVL = 15 mm, fig. 3; UMMZ 189900, SVL = 9 mm) show the postorbitofrontal as a single ossification extending back with its tapering posterior process up to the squamosal, with which it narrowly overlaps; the latter bone still fails to contact the quadrate posteriorly. The ventral process of the postorbitofrontal contacts the posterior dorsal process of the jugal, which now completes the postorbital arch. The prefrontal ossification has developed a narrow ventral process, mapping the anterolateral margin of the orbit and meeting the palatine ossification ventrally. Both the jugal and the maxillary bones continue to show delayed ossification along the course of the superior alveolar nerve. Also, the tooth-bearing ventral margin of the maxillary bone continues to remain separated from the as yet only weakly ossified ascending process. The premaxillary is now more completely ossified and carries distinct lateral and nasal (dorsal) processes. Between the premaxilla and the maxilla, the ossified septomaxilla has made its appearance. The nasal bone still fails to contact the premaxilla anteriorly and the frontal posteriorly, and, whereas the frontal bones are more advanced in ossification than the parietals, they still fail to meet in the dorsal midline of the skull. Meckel's cartilage is now completely covered by dermal bone, at least in lateral view.

Apart from the appearance of new dermal ossifications (postorbitofrontal and septomaxilla), this stage of skull development (UMMZ 189899, 189900) also shows progress in endochondral ossification. The retroarticular process shows the be-

ginning of endochondral ossification immediately behind the articular facet. Endochondral ossification has also started in the middle portion of the shaft of the quadrate, in the middle portion of the ascending process of the palatoquadrate (epipterygoid), and in the middle portion of ceratobranchial I. Specimen MHNG 806.58a shows that endochondral ossification of the quadrate and epipterygoid slightly precedes ossification of ceratobranchial I.

Specimen UMMZ 189900 shows that the first indication of endochondral ossification of the braincase is in the occipital arch, the presumptive exoccipital. Specimen UMMZ 189989 demonstrates that the ossification of the exoccipital is followed by the onset of endochondral ossification in the basal plate behind the fenestra basicranialis (the presumptive basioccipital) and in the area of the acrochordal cartilage (sella turcica and dorsum sellae, parts of the presumptive basisphenoid). At this stage, weak perichondral ossification can be observed to affect the tectum synoticum (the presumptive supraoccipital) as well as the dorsal tip and caudal margin of the otic capsule. Specimen UMMZ 189895 (SVL = 11 mm) shows that perichondral ossification along the prominences of the semicircular canals precedes that of the tectum synoticum.

The last elements of the dermatocranium to appear are the ectopterygoid (MHNG 806.58a) and, still later, the lacrimal (UMMZ 189895, MHNG 806.58b). As endochondral ossification of the braincase advances, the supraoccipital ossification spreads across the tectum synoticum to include the dorsal tip of the otic capsules (housing the crus communis of the labyrinth). The prootic starts endochondral ossification at the anterior tip of the otic capsule, housing the ampulla of the anterior semicircular canal; the opisthotic starts endochondral ossification at the posterior tip of the otic capsule, housing the ampulla of the posterior semicircular canal. The central part of the otic capsule, surrounding the fenestra vestibuli, remains cartilaginous.

As *Lacerta vivipara* approaches or reaches the newborn stage (UMMZ 189898, MBS 14918), all elements of the dermatocranium are present. The dermal covering of the snout is complete (fig. 4), and the sutures between the anterior parts of the frontals, prefrontals, nasals, maxillae, and premaxilla are closed. The anterior (interorbital) parts of the frontals meet in the dorsal midline of the skull, but the posterior parts remain slender and widely divergent, meeting the still narrow and

characteristically triradiate ossifications of the parietals. The posterior margin of the parietal skull table is still incomplete in UMMZ 189898. There is no dermal covering of the brain (except for the tractus olfactorii) in the newborn *Lacerta* (see also Rieppel, 1984). The elements of the postorbital and upper temporal arch are all complete, but the dermal roofing of the upper temporal fenestra (by a broadening of the posterior process of the postorbitofrontal) is incomplete. The dermal ossifications of the palate and of the lower jaw are complete, and the scleral ossicles have ossified.

Of the splanchnocranium, the epipterygoid and ceratobranchial I are both well ossified. Both the shaft and the lateral conch of the quadrate are well ossified, but the broad dorsal surface of the cephalic condyle and the entire mandibular condyle remain cartilaginous. Although the extent of cartilage will become reduced during subsequent development, no separate epiphyseal ossification centers have been observed to form in these two bones (Dollo, 1884, p. 70, mentions the observation of an epiphysis on the dorsal head on the quadrate in an unspecified lizard).

Of the braincase, the basioccipital and the basisphenoid are well ossified in the newborn lizard, but between the two bones persists a wide open fontanelle representing the fenestra basicranialis. All other braincase elements (exoccipital, supraoccipital, prootic, and opisthotic) remain separated by broad cartilaginous zones of growth. Although the foramen for the facialis nerve is enclosed in the prootic ossification, the latter remains widely separated from the basisphenoid; cartilage also forms the lower margin of the fenestra vestibuli as well as the lateral margin of the basicranial fenestra between the basisphenoid and basioccipital ossifications. The Vidian canal is closed at this stage by the lateral wings of the parasphenoid underlying the basitrabecular processes.

The major changes that occur during postembryonic growth of *Lacerta* are closure of the sutures between the braincase elements and closure of the dermal skull roof. The ossifications along the posterior margins of the parietal meet and fuse in the dorsal midline of the skull at an SVL of about 24.5 mm (NMBE 1'001'297); the skull table closes up in advanced stages with an SVL of about 27–29 mm. The frontoparietal suture is closed in specimen MBS 5625 with an SVL of 34 mm, but a large longitudinal fontanelle continues to subdivide the parietal skull table, extending backward to include the prospective pineal foramen. Behind this point, the parietals are fused already.

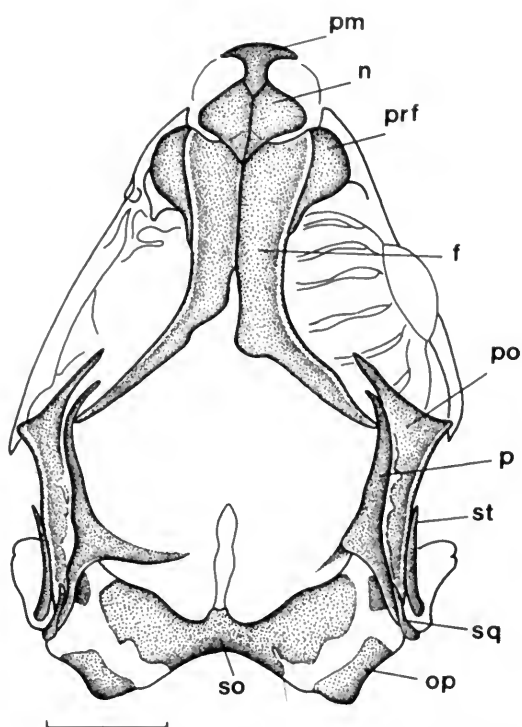


FIG. 4. The dermatocranium of *Lacerta vivipara* (UMMZ 189898, SVL* = 19 mm) in dorsal view. Scale bar = 1 mm. Abbreviations: f, frontal; n, nasal; op, opisthotic; p, parietal; pm, premaxilla; po, postorbitofrontal; prf, prefrontal; so, supraoccipital; sq, squamosal; st, supratemporal.

THE VERTEBRAE AND RIBS—The first indication of ossification of the vertebrae is observed in specimens UMMZ 189899 (SVL = 15 mm) and UMMZ 189900 (SVL = 9 mm), after ossification in the appendicular skeleton has started. In specimen UMMZ 189906 (SVL = 7 mm), the axial skeleton shows no indications of ossification at this stage, yet the clavicles have started to form and narrow zones of endochondral ossification have developed in the stylopodial and zeugopodial elements of the forelimbs and hind limbs as well as in the central metacarpals and metatarsals.

Ossification of the vertebrae proceeds along a distinct anteroposterior and ventrodorsal gradient. At a stage (UMMZ 189899) when ossification of the cervical vertebrae is already well advanced, ossification of the caudal vertebrae may not even have begun, while in the presacral region ossification remains restricted to progressively more ventral parts of the centrum. The early ossification of vertebral elements primarily affects the ventral part of the centrum; continuing ossification spreads

in a dorsal direction into the base of the neural arch. The neural spine and the pre- and postzygapophyses remain cartilaginous until relatively late during development. A broad zone of cartilage continues to separate the centrum from neural arch ossification, representing an early stage of the neurocentral suture incorporating the transverse process (diapophysis [or synapophysis] *sensu* Hoffstetter & Gasc, 1969). The cartilaginous proximal head of the ribs is separated from the tip of the cartilaginous transverse process by a distinct articulation. This is not apparent in sacral “ribs” and in the transverse process of the caudal vertebrae, which are continuous with the cartilage of the respective vertebral element. As ossification spreads toward the basal part of the neural arch, it will initially extend over the dorsal surface of the sacral “ribs” and transverse processes, leaving no gap (cartilaginous suture) between these structures and the neural arch in dorsal view. Inspection from ventral view during these stages of ossification reveals an as yet unossified ventral surface of sacral “ribs” and transverse processes that merges into the broad neurocentral suture passing below these elements.

The neurocentral suture remains open until postembryonic development. Perichondral ossification of the presacral transverse processes (diapophyses) has started in the newborn stage (MBS 14918), where it spreads across the dorsal surface in continuity with the ossification of the base of the neural arch, while the ventral surface remains cartilaginous and confluent with the neurocentral suture—as was described above for the sacral ribs and transverse processes of the caudal vertebrae. At a later stage (UMMZ 189898), the ventral surface of the diapophyses is also affected by (perichondral) ossification, with the result that the neurocentral suture now runs ventral to the diapophyses, sacral vertebrae, and caudal transverse processes. It will eventually close in an anteroposterior sequence, starting in specimen MHNG 806.53 (SVL = 31.5 mm).

In UMMZ 189900 (SVL = 9 mm), with advanced ossification of the cervical vertebrae, the first signs of rib ossification appear. The first cervical rib (associated with the fourth cervical vertebra) and the second show no sign of ossification, but the third, fourth, and fifth cervical ribs show perichondral ossification in their proximal “shoulder” region. Within the sternal and dorsal ribs perichondral ossification decreases continuously in an anteroposterior direction. Ossification of the ribs lags behind that of the vertebrae and does not

follow the anteroposterior gradient manifest in vertebral ossification.

In *Lacerta vivipara*, cartilaginous transverse processes on caudal vertebrae develop in an anteroposterior sequence after anterior elements of the axial skeleton have already begun to ossify. In specimen UMMZ 189906 (SVL = 7 mm), with no ossification in the axial skeleton, well-developed (cartilaginous) transverse processes are present on caudal vertebrae 1–5, and rudimentary processes on vertebrae 6–7 or 8. More transverse processes have been preformed in cartilage in specimen UMMZ 189899 (SVL = 15 mm), when ossification is well under way in the presacral vertebral column, but their exact number is difficult to determine because of their small size. In specimen UMMZ 189895 (SVL = 11 mm), at a stage when sacral ribs and anterior transverse processes have already started to ossify, cartilaginous processes can be identified up to the sixteenth caudal vertebra. Ossification of the transverse processes is continuous with the base of the neural arch and proceeds in a proximodistal direction within the individual transverse process. In the newborn specimen MBS 14918, the transverse processes of caudal vertebrae 1–4 show endochondral ossification, while those of caudal vertebrae 5–7 show perichondral ossification only, decreasing in a posterior direction. It is at this stage or slightly earlier (MHNG 806.58b, perichondral ossification in sacral ribs and anterior transverse processes only) that the chevron bones (haemapophyses) show the first indication of ossification. They again ossify along an anteroposterior gradient. Endochondral ossification starts in the midportion of the paired limbs of the haemapophyses, from where it spreads toward the distal tip and the proximal articular heads.

Appendicular Skeleton

THE PECTORAL GIRDLE—The first elements of the pectoral girdle to ossify are the clavicles (in specimen UMMZ 189906, SVL = 7 mm), at a time when the postcranial axial skeleton has not yet started to ossify, but when endochondral ossification has replaced the cartilage in the middiaphyseal region of stylopodial and zeugopodial elements in both front limbs and hind limbs. In specimen UMMZ 189900 (SVL = 9 mm) the interclavicle has started to ossify, and perichondral ossification is observable around the constricted midportion of the scapula, bone starting to replace cartilage in a small patch on the caudal margin of

the midportion of the scapula. Ossification within the scapula will spread from there through the midportion of the element (fig. 5) and eventually into the dorsal wing and toward the glenoid fossa. The timing of ossification of the interclavicle and scapula relative to axial elements is variable: it has not yet started in specimen MHNG 806.58a, where ossification of the presacral vertebral column is well advanced, and is only just beginning in specimen MHNG 806.58b, where ossification of the axial skeleton has progressed into the proximal caudal region. The last element of the pectoral girdle to ossify is the coracoid, starting, in specimen UMMZ 189898 (SVL = 19 mm), around the supracoracoid foramen and along the posterior margin of the anterior coracoid fenestra (fig. 6).

The clavicle first appears as a simple, sigmoidally curved rod (UMMZ 189906, MHNG 806.58a). It then broadens medially (UMMZ 189900), or develops a hook-like proximal curvature instead (UMMZ 189899), mapping the medial margin of the prospective clavicular perforation. In specimen UMMZ 189895 (fig. 6a) the clavicle is broad but only lightly ossified medially, with well-ossified margins along the anterior, proximal, and posterolateral margins of the prospective perforation. The ossification of the caudal margin of the clavicular perforation is somewhat delayed, as is also the case in the newborn stage MBS 14918. Specimen UMMZ 189898 (fig. 6b) shows a complete clavicular perforation on the left side, but a gap in its posterior margin on the right side. The formation of the perforated clavicle is therefore variable to some degree. Starting out as a slender ossification, the medial portion of the bone may or may not expand to map the future shape of the bone. Ossification proceeds around the anterior and medial margins of the perforation, closing it posteriorly at a relatively late stage of development.

The interclavicle first is represented by its anteriormost tip only, lying between the two medial parts of the clavicles. In specimen UMMZ 189899 the clavicle has assumed its cruciform shape, but ossification is most pronounced in its anterior tip. The interclavicle grows by apposition, which increases the relative length of the posterior and lateral processes.

THE PELVIC GIRDLE—The first element of the pelvic girdle to start ossification is the ilium, followed by the pubis and the ischium. This sequence of ossification is constant, but the relative timing of ossification of pelvic elements with respect to

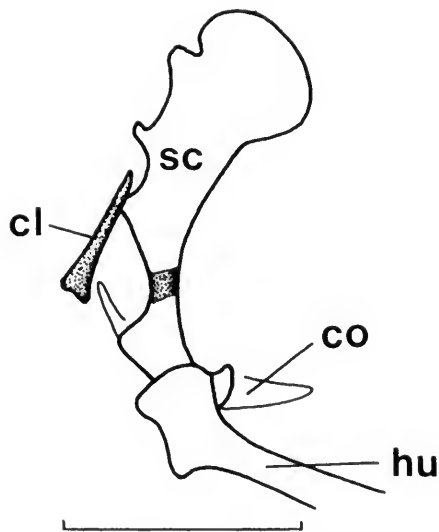


FIG. 5. The pectoral girdle of *Lacerta vivipara* (UMMZ 189899, SVL* = 15 mm) in left lateral view. Scale bar = 1 mm. Abbreviations: cl, clavicle; co, coracoid; hu, humerus; sc, scapula.

other parts of the skeleton is variable. In no instance, however, does the ilium start ossification before the clavicles. In specimen UMMZ 189899, the ilium is the only element to have started ossification at a stage when the clavicles, the interclavicle, and the scapula have already started ossification. In specimen UMMZ 189900 there is extensive perichondral but only minimal endochondral ossification in the ilium, and only perichondral ossification in the pubis, while the dermal clavicle, interclavicle, and endochondral scapula all have started ossification. Specimen MHNG 806.58a appears characterized by a delayed

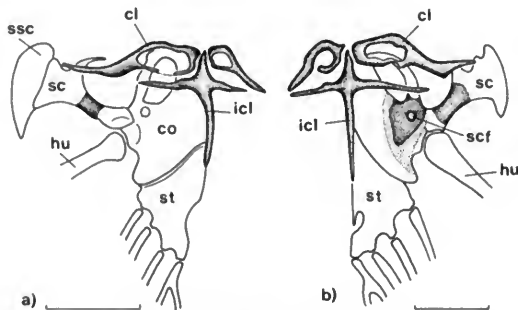


FIG. 6. The pectoral girdle of *Lacerta vivipara* in ventral view. a, UMMZ 189895, SVL* = 11 mm; b, UMMZ 189898, SVL* = 19 mm. Scale bar = 1 mm. Abbreviations: cl, clavicle; co, coracoid; hu, humerus; icl, interclavicle; sc, scapula; scf, supracoracoid foramen; st, sternum.

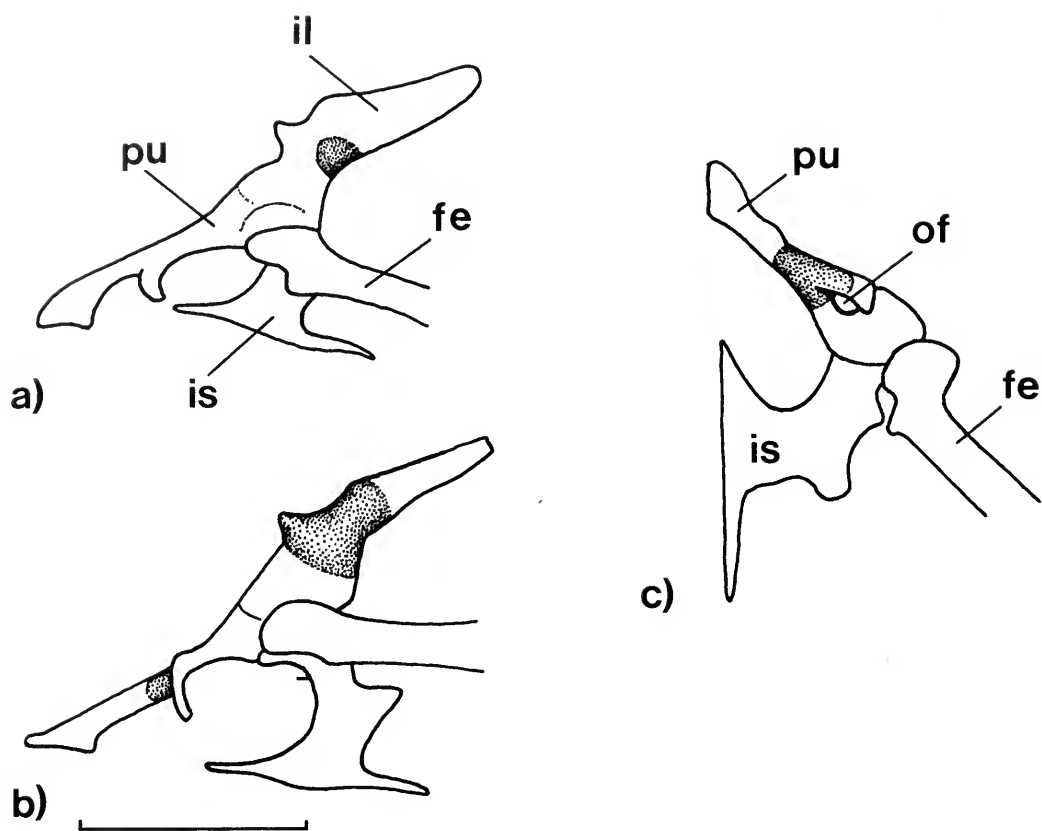


FIG. 7. The pelvic girdle of *Lacerta vivipara*. **a**, UMMZ 189899, SVL* = 15 mm, left lateral view; **b**, UMMZ 189895, SVL* = 11 mm, left lateral view; **c**, UMMZ 189895, SVL* = 11 mm, ventral view. Scale bar = 1 mm. Abbreviations: fe, femur; il, ilium; is, ischium; of, obturator foramen; pu, pubis.

ossification of the pectoral girdle, the clavicles being the only elements that have started ossification when endochondral ossification is present in both the ilium and pubis.

The first indication of ossification in the ilium is a perichondral covering around its middle portion, between the acetabulum and the dorsal wing. Endochondral ossification begins at the posterior margin of the ilium, at about the height of the preacetabular process (fig. 7a). From there it expands through the middle portion of the bone, including the preacetabular process but not yet affecting the dorsal wing (articulating with the sacral ribs) and the ventral portion (participating in the formation of the acetabulum) (fig. 7b). In the newborn (MBS 14918), the ilium is well ossified except for its posterior tip and the parts participating in the acetabulum.

The first indication of ossification in the pubis is a perichondral covering around its middle portion just below the obturator foramen and includ-

ing the base of the pectineal tubercle. This is also the area in which endochondral ossification starts, lining the ventral margin of the obturator foramen and including the base of the pectineal tubercle (figs. 7b,c). In the newborn (MBS 14918), the obturator foramen still remains incompletely closed (dorsally) by endochondral ossification. In specimen UMMZ 189898 (SVL = 19 mm), the obturator foramen is fully enclosed by endochondral bone.

The first indication of endochondral ossification in the ischium (MHNG 806.58b, SVL = 20.5 mm) is at its anterior edge, rather than at the posterior edge as seen in the scapula or ilium. This may be explained by the fact that the anterior edge of the ischium represents, morphologically, the posterior margin of the thyroid fenestra, and endochondral ossification starts around foramina or fenestrae in the pubis (ventral margin of the obturator foramen) and coracoid (around the supracoracoid foramen and along the posterior margin of the anterior coracoid fenestra).

THE FORELIMB—In all long bones of tetrapods, perichondral ossification of the diaphyses precedes endochondral ossification. Endochondral ossification invariably starts at middiaphysis and spreads symmetrically toward the epiphyseal heads of the bones. This contrasts with carpal (tarsal) elements, which undergo endochondral ossification directly.

A narrow zone of endochondral ossification is observed in the humerus, radius, and ulna at a stage when only the clavicles, among girdle elements, have started to ossify (UMMZ 189906, SVL = 7 mm); stylopodial and zeugopodial elements apparently start ossification more or less simultaneously. At the same time there is perichondral ossification in the diaphysis of metacarpals (mc) 2–4, very faint perichondral ossification in mc1 and in most phalanges except for the unguals, but no sign of beginning ossification in mc5 or in any of the carpal elements. Specimen UMMZ 189900 (SVL = 9 mm) has not progressed beyond this stage of ossification, but it shows that perichondral ossification is more pronounced in mc3 and mc4, as compared to mc2, and is only just beginning in mc1 and in the phalanges.

In specimen UMMZ 189899 (SVL = 15 mm), endochondral ossification has increased in the diaphysis of the humerus, radius, and ulna. There is a narrow zone of endochondral ossification in the middiaphyseal area of mc3, only just beginning endochondral ossification in mc4, still only perichondral ossification in mc1 and mc2, and faint perichondral ossification in mc5 and in the phalanges (except the unguals). Other specimens corroborate the predominance of the third digit (metacarpal) in ossification: in MHNG 806.58a (SVL = 16.5 mm), mc3 is the only element of the carpus to show endochondral ossification; MHNG 806.58b (SVL = 20.5 mm) shows advanced endochondral ossification in mc3, beginning endochondral ossification in mc4, and only perichondral ossification in mc2. The newborn stage MBS 14918 shows a gradient of endochondral ossification with mc3 > mc4 > mc2, perichondral ossification in mc1, and no ossification as yet in mc5, but perichondral ossification in all the phalanges including the unguals, with cartilage degeneration beginning in the diaphyseal region. There may be some variability, as exemplified by specimen UMMZ 189895, where endochondral ossification is pronounced in mc2, mc3, and (least advanced) mc4 in the right hand, while mc3 is the only metacarpal showing endochondral ossification as yet in the left manus. UMMZ 189898 is the only specimen documenting a somewhat more advanced degree of endochondral os-

sification in mc4 as compared to mc3 and mc2. Specimen UMMZ 189896 (SVL = 22 mm) shows advanced endochondral ossification in the diaphysis of all metacarpals and phalanges, leaving only the carpal bones and epiphyses to ossify during postnatal growth.

In summary, the humerus, radius, and ulna are the first elements of the forelimb to start endochondral ossification, followed by the metacarpals and phalanges. Within the metacarpal series, there is a distinct predominance of the digit 3, followed in sequence by mc4 > mc2 > mc1 > mc5. No distinct predominance of the third or any other digit is observed in the more or less simultaneous ossification of phalanges; the unguals, however, lag behind more proximal phalanges in ossification. Metacarpal 5 and all carpal elements, as well as all epiphyses, ossify during postnatal growth.

THE HIND LIMB—The earliest stage of ossification in the hind limb (UMMZ 189906, SVL = 7 mm) shows beginning replacement of cartilage in the middiaphyseal region of the femur, tibia, and fibula, simultaneous with the ossification of serially homologous elements in the forelimb. There is perichondral ossification in metatarsals (mt) 1–4, none in mt5, and very slight perichondral ossification in the diaphysis of the phalanges except for the unguals. There is, therefore, a slight advance in perichondral ossification in the autopodial elements of the hind limb as compared to the forelimb, a tendency that will become more accentuated during subsequent development for all elements except for mt5.

In the next stage available (UMMZ 189900, SVL = 9 mm), there is endochondral ossification in the diaphysis of mt4 and mt3, a narrow zone of cartilage replacement in mt2, weak perichondral ossification in mt1 and in the phalanges (except the unguals), but no sign of ossification in mt5. Specimen UMMZ 189899 (SVL = 15 mm) shows a distinct gradient of endochondral ossification with mt3 > mt4 > mt2, perichondral ossification in mt1 and in the phalanges (except unguals), but again no sign of ossification in mt5. Specimen UMMZ 189895 (SVL = 11 mm) is the first to show a narrow zone of endochondral ossification in mt1 (right foot only; beginning cartilage degeneration in left foot), a stage at which some cartilage cell degeneration can be observed to start in the diaphysis of phalanges (except the unguals) but at which mt5 has not yet started ossification (same in MHNG 806.58b). Specimen MHNG 806.58a (SVL = 16.5 mm) shows endochondral ossification to

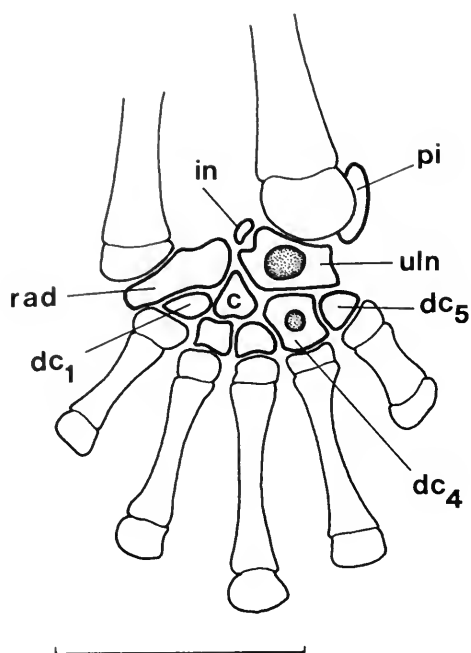


FIG. 8. The left carpus of *Lacerta vivipara* (NMBE 1'001'297, SVL = 24.5 mm) in dorsal view. Scale bar = 1 mm. Abbreviations: c, centrale; dc 1–5, distal carpals 1–5; in, intermedium *sensu* Born (1876); pi, pisiforme; rad, “radiale”; uln, ulnare.

be advanced in mt2–mt4, less advanced in mt1, and just beginning in mt5 (same in UMMZ 189898). Ossification of mt5 does not begin in the mid-diaphyseal region but, rather, on its medial border facing the proximal head of mt4, at the base of the medial plantar tubercle. Again, some variability must be accounted for, because in the newborn stage MBS 14918, the diaphyses of mt2–mt4 have been completely replaced by bone, whereas only the middle part is ossified in mt1, and mt5 remains unossified. At this stage endochondral ossification has started in some phalanges, being most advanced in the proximal phalange of digits 3 and 4. It is at this stage that the first tarsal element, the astragalus, starts ossification. In UMMZ 189896 (SVL = 22 mm), the diaphyses of mt1–mt4 are all well ossified, while endochondral ossification of mt5 still remains restricted to the inner side facing the proximal head of mt4; perichondral ossification has spread to cover most of the midregion of the element. The diaphyses of the phalanges are well ossified, as are the unguals, whereas the astragalus remains the only tarsal bone to have started ossification. Epiphyseal ossification has not yet started.

Similar to the pattern observed in the forelimb, the femur, tibia, and fibula are the first elements

to start more or less simultaneous endochondral ossification in the hind limb, followed by the metatarsals and the phalanges. Within the metatarsal series, there is again a predominance of digit 3 in ossification, followed in sequence by mt4 > mt2 > mt1 > mt5, the latter's ossification being much delayed. Endochondral ossification of the phalanges, even if less sequential than that of metatarsals, supports some predominance of central over peripheral digits. In general, autopodial elements of the hind limb precede those of the forelimb in ossification, the astragalus starting ossification prior to any of the carpal elements.

The Postembryonic Ossification of Carpal and Tarsal Elements

The carpus of *Lacerta vivipara* includes a total of 10 cartilaginous precursors of later ossifications (fig. 8): an ulnare lies at the distal end of the ulna, the pisiforme lies posterolateral to the distal end of the ulnare, and the “radiale” (see discussion below of fusion of precursor elements) appears to be represented by a single chondrification with a narrow limb lying distal to the radius and a somewhat expanded lateral head lying distal to the spatium interosseum separating the radius and ulna. A separate intermedium cartilage is observed between the distal heads of the radius and ulna (Born, 1876), and a centrale is present, as are distal carpals (dc) 1–5.

Cartilage precursors in the tarsus are less numerous, partly due to the fact that whatever the number and homologies of proximal elements (see discussion in Mathur & Goel, 1976, and Shubin & Alberch, 1986), they all fuse into a single proximal tarsal cartilage during development (Gegenbaur, 1864, pp. 64, 73, 87; Born, 1876, 1880; Baur, 1885; Sewertzoff, 1908). The astragalus and calcaneum will ossify within this “*tarsale proximale*” (Sewertzoff, 1908), each from a separate ossification center. The complex tongue-in-groove joint between the astragalocalcaneum and the fourth distal tarsal, characteristic of adult squamates (Schaeffer, 1941; Brinkman, 1980), is preformed in cartilage. Two additional cartilage elements are the precursors of the distal tarsals (dt) 3 and 4.

All carpal and tarsal bones start ossification endochondrally. The first element to start ossification (at the newborn stage) is the astragalus (MBS 14918, UMMZ 189896), preceding the ossification of any carpal bone. It appears as a small circular ossification within the proximal tarsal cartilage in an intermedium position, i.e., distal to the spatium interosseum separating the tibia and fibula. The

second element to start ossification is dt4, which in specimen FMNH 66933 (SVL = 20 mm) is distinctly more advanced in ossification than the calcaneum. The latter is represented by a second small and circular ossification in the proximal tarsal cartilage, distinctly less advanced than the astragalus and lying distal to the fibula. The fourth and last element in the tarsus to ossify is dt3 (NMBE 1'001'296, SVL = 22 mm). The great majority of postembryonic stages investigated show a distinct gradient of ossification of tarsal elements, with astragalus > dt4 > calcaneum > dt3. There are only two exceptions: in specimen MBS 4240, dt3 is absent (the ossification gradient being astragalus > dt4 > calcaneum), whereas in specimen NMBE 1'001'297 (SVL = 24.5 mm), dt3 starts ossification prior to the calcaneum (fig. 9). During subsequent growth, the astragalus and calcaneum increase in size and assume their characteristic shape and structure; in specimen MBS 5949 (SVL = 30 mm), the two bones are sutured to one another. Their fusion takes place at a later age, no longer represented in the sample investigated.

The first element in the carpus to ossify is the ulnare. It first appears in specimen FMNH 66933 (SVL = 20 mm), at a stage when the astragalus, dt4, and the calcaneum have already started ossification. The second element to ossify (in NMBE 1'001'297, SVL = 24.5 mm) is dc4, at a stage when dt3 has started ossification. Beyond that stage, the ossification sequence of carpal elements is somewhat variable, although the majority of the specimens investigated support a sequence starting with the ulnare > dc4 > dc3 and centrale (simultaneous) > dc2 > "radiale" > dc5 > pisiforme > dc1 > intermedium. The intermedium (*sensu* Born, 1876) remains unossified in specimen MBS 5625 (SVL = 34 mm) at a stage when all other carpal and tarsal elements are well ossified except dt1, in which ossification is only just beginning. Notable exceptions to this typical sequence are seen in three specimens. In FMNH 78365, there is an early ossification of the pisiforme and of the "radiale" at a stage when dc1, dc2, and dc5 show no sign of ossification. In NMBE 1'001'299, the left manus shows the ossification of the pisiforme to precede that of dc5. Specimen NMBE 1'001'298 finally shows the ossification in the "radiale" to be more advanced than in dc2.

In summary, there is a dominance of the astragalus in the ossification process of the tarsus, originating in an intermedium position and followed by the ossification of dt4, whereas the precedence of ossification in the carpus is on the ulnar

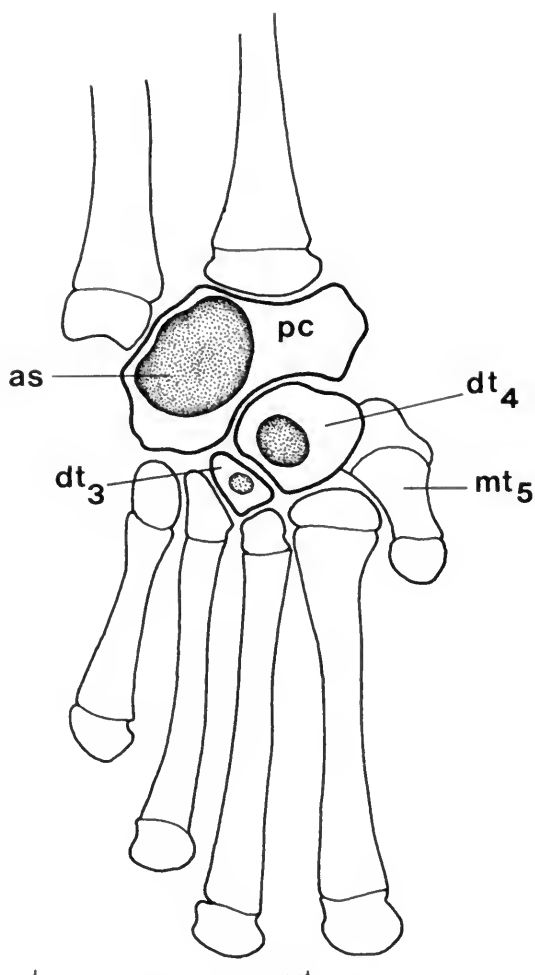


FIG. 9. The left tarsus of *Lacerta vivipara* (NMBE 1'001'297, SVL = 24.5 mm) in dorsal view. Scale bar = 1 mm. Abbreviations: as, astragalus; dt 3-4, distal tarsals 3-4; mt5, metatarsal 5; pc, proximal tarsal cartilage.

side of the autopodium, the ulnare being the first element to ossify, followed by dc4 (see also table 2).

The Ossification of Epiphyses

The first epiphyses to start calcification in the forelimb are those on the proximal and distal heads of the femur (in NMBE 1'001'298, the epiphysis has started to calcify on the proximal head of the humerus only, which precedes calcification of the distal epiphysis), followed by calcification of the epiphyses on the proximal (olecranon) and distal heads of the ulna, but not of the radius (MHNG 806.53; MBS 5652, 5949, 11898, 16487; NMBE 1'001'299). Calcification of the epiphyses on the

TABLE 2. The sequence of ossification of carpal and tarsal elements in *Lacerta vivipara*.

postembryonic (postnatal) stages	astragalus	dt 4	calcaneum	dt 3	ulnare	dc 4	dc 3	centrale	dc 2	radiale	dc 5	pisiforme	dc 1
MBS 14918: 17.5mm ¹⁾	+	0	0	0	0	0	0	0	0	0	0	0	0
FMNH 66933: 20mm	+	+	+	0	+	0	0	0	0	0	0	0	0
NMBE 1'001'297: 24.5mm	+	+	0	+	+	+	0	0	0	0	0	0	0
MBS 4240: 27.5mm	+	+	+	?	+	+	+	+	+	0	0	0	0
FMNH 78365: 29mm	+	+	+	+	+	+	+	+	0	+	0	+	0
MBS 15949: 27mm ²⁾	+	+	+	+	+	+	+	+	+	+	0	0	0
MHNG 806.53: 31.5mm	+	+	+	+	+	+	+	+	+	+	+	0	0
MBS 5949: 30mm ³⁾	+	+	+	+	+	+	+	+	+	+	+	+	0
MBS 5625: 34 mm	+	+	+	+	+	+	+	+	+	+	+	+	+

1) UMMZ 189896, 22 mm.

2) NHBE 1'001'298, 26.5 mm.

3) MBS 16487, 33 mm; MBS 11898, 33.5 mm.

radius seems much delayed and is not apparent in the sample investigated. As the epiphyses calcify on the ulna, they also start to calcify on the distal heads of the metacarpals. The epiphyses on the five distal heads of the metacarpals ossify within a brief period of time and almost simultaneously; FMNH 78365 is the only specimen that shows calcification in the epiphyses of mc1, mc2, and mc4, but not on the distal heads of mc3 or mc5. All others show the simultaneous beginning of epiphyseal calcification in the distal heads of the metacarpals prior to calcification in the proximal heads of the same elements. The proximal metacarpal epiphyses show a greater degree of resolution in their pattern of calcification than the distal epiphyses, starting with mc1 (MBS 5949; MBS 5625, right manus), followed by mc2 (NMBE 1'001'299; MBS 11898, right manus), followed by mc3 (MBS 16487; MBS 11898, left manus), followed by mc4 and mc5 (MBS 5625, left manus).

Calcification of epiphyses in the phalanges is much delayed as compared to the metacarpals, and the material at hand does not permit the establishment of any sequence, or show the predominance of any particular digit. MBS 16487 is the only specimen in which most of the phalangeal

epiphyses are calcified; separate calcification centers remain restricted to the proximal heads of the phalanges (as already noted by Dollo, 1884, and Moodie, 1908).

The onset of calcification of epiphyses in the hind limb generally precedes that in the forelimb. It starts on the proximal and distal heads of the femur, followed by the distal head of the fibula and distal heads of the metatarsals. Calcification of the distal head of the tibia is delayed until all distal and some proximal heads of the metatarsals have already started epiphyseal calcification.

The first epiphysis in the metatarsal series of elements to start calcification is on the distal head of mt4 (NMBE 1'001'298), followed by the distal head of mt3 and mt2 (MBS 15949). At that stage, calcification of proximal epiphyses begins. The distal epiphyses on mt1 and, last, of mt5 start calcification only after calcification has started in the proximal heads of mt1-mt4. Within the proximal metatarsal heads, there is a clear sequence of calcification progressing from mt1 (MBS 5625, right foot) to mt2 (NMBE 1'001'299), to mt3 (MBS 5949), to mt4. Calcification in the proximal head of mt5 is much delayed, but when it begins, it can be observed to form two separate epiphyseal centers.

The first one to calcify caps the outer process and may more appropriately be called an apophyseal calcification (ossification) center; the second calcification develops on the medial aspect of the mt5 head, articulating with dt4.

Phalangeal epiphyses start calcification at a later stage, with no apparent regularity of pattern or sequence documented in the sample. Phalangeal epiphyses are distinct on the proximal heads only, but, in contrast to Dollo (1884) and Moodie (1908), some specimens provide evidence of a separate epiphyseal calcification on the distal ends of the proximal phalange in digit 4 (MHNG 806.53), digits 3 and 4 (NMBE 1'001'299), or digits 2–4 (NMBE 1'001'298). The only difference to epiphyseal calcifications in proximal phalangeal heads is the narrowness of the metaphysis, which is not apparent in the distal heads of other phalanges at all. This suggests that the distal phalangeal heads normally calcify/ossify not from a separate center, but from the metaphysis, as suggested by de Ricqlès (1976) for *Sphenodon*.

The postembryonic calcification of epiphyses is not as regular in terms of pattern and sequence as is the onset of diaphyseal ossification. Where some regularity can be established, however, epiphyseal calcification does not necessarily follow the sequence of diaphyseal ossification. In the metatarsals, for example, calcification of the distal heads corresponds rather closely to the sequence of diaphyseal ossification, whereas calcification of the proximal heads proceeds in an opposite sequence. The same is true for the proximal heads of the metacarpals.

Discussion

Osteogenesis in the Skull

The most complete account of the development of the osteocranium in lizards is that of Gaupp (1909), who provides details on the shape and location of elements at their first appearance but no information on the sequence of ossification. A number of studies (Peyer, 1912; Bäckström, 1931; Franklin, 1945; Pringle, 1954) have provided a fairly detailed knowledge of the sequence of ossification of cranial elements in snakes, most recently improved and summarized by Haluska and Alberch (1983). One dominant feature of osteogenesis in the *Lacerta* skull is the early appearance of dermal elements associated with the mandib-

ular arch (dermal palate and lower jaw) and of dermal elements of the upper jaw. The same is true for fishes (Dunn, 1984) and, to some degree, for birds (Schinz & Zangerl, 1937). Earlier studies based on histological techniques showed the pterygoid, the palatine, and some of the lower jaw elements to start ossification before the premaxilla and maxilla (in *Lacerta sicula*: Rieppel, 1987b). The palatine and the pterygoid bones are also the first to start ossification in the snake skull (Franklin, 1945, p. 71; Haluska & Alberch, 1983), followed by bones associated with Meckel's cartilage. In the snake *Elaphe* (Haluska & Alberch, 1983), the ectopterygoid appears earlier than in *Lacerta*. However, Franklin (1945) described a late appearance of the ectopterygoid in *Natrix*.

Haluska and Alberch (1983) describe in detail the ossification of the maxilla from several centers. Admitting that it may be difficult to define true foci of ossification if calcium is irregularly deposited in a collagenous matrix, they claim to have identified at least two such centers (Haluska & Alberch, 1983, p. 54). *Lacerta vivipara* also has a very irregular ("patchy") ossification of the maxilla. Irregularity renders it impossible to define centers of ossification along the tooth-bearing ventral margin, and the ascending process of the maxilla appeared to ossify independently from the latter during early stages of development. Along the course of the superior alveolar nerve, broad and irregularly shaped unossified lacunae persist in the tooth-bearing ventral margin of the maxilla until late during embryonic development. They later form an irregularly spaced series of small foramina for the passage of labial branches of the superior alveolar nerve.

A number of details concerning the development of the *Lacerta* dermatocranium seem worthy of further comment. The lacrimal bone becomes reduced, or is lost, in a number of lizards, which is in accordance with its late appearance. The jugal bone starts ossification in its anteriormost (suborbital) portion in *Lacerta*, which contrasts with its reduced morphology in other lizards such as the fossorial acontine scincomorphs, where the jugal may form a complete postorbital arcade, or may be reduced to a small splint of bone attached to the posterior end of the maxilla, with no suborbital (maxillary) process (Rieppel, 1981, 1982). In *Lacerta*, the supratemporal ossifies before the squamosal. In Gekkotans, where only one of the two elements may be retained, this is usually interpreted as squamosal (Kluge, 1967), whereas the supratemporal rather than the squamosal is be-

lied to persist in the genus *Anniella* and in snakes. As in the newborn *Lacerta*, the skull of a hatching *Cyrtodactylus* shows a wide open fontanelle in the dermal (parietal) skull roof (Rieppel, 1992b), as seems to be typical for all lizards, indeed most vertebrates (Hanken, pers. comm.; see Rieppel, 1984, for exceptions among squamates).

The first neurocranial component to ossify both in *Lacerta* and in snakes (Franklin, 1945; Haluska & Alberch, 1983) is the occipital arch, i.e., the exoccipital. The basicranial elements of *Lacerta* and snakes then start endochondral ossification before such occurs in the otic capsule or tectum synoticum.

Osteogenesis in the Axial Skeleton

In *Lacerta*, ossification in the skull starts before ossification of the vertebral column; even the clavicles, as well as the stylopodial and zeugopodial elements of the forelimb and hind limb, start ossification before the vertebrae. This is identical to the sequence of osteogenesis in the chick, as described by Lillie (1919), but is in marked contrast to the sequence in snakes (*Thamnophis*: Franklin, 1945), where the anterior cervical vertebrae are the first skeletal elements to start ossification.

Ossification of the vertebral column and associated structures proceeds along a distinct anteroposterior gradient, as was also recorded for the gekkonid lizard *Cyrtodactylus pubisulcus* (Rieppel, 1992b), snakes (Franklin, 1945), and the chick (Lillie, 1919). As in snakes (Franklin, 1945), the onset of ossification in the ribs lags somewhat behind that in the vertebral column. In lizards, ossification of sacral ribs and caudal transverse processes is continuous with ossification of the neural arch and related, in its extent, to the successive closure of the neurocentral suture. In both *Sphenodon* and *Alligator*, the sacral ribs and caudal transverse processes ossify from separate ossification centers (Rieppel, 1992b); recent observations showed the transverse processes of the presacral vertebrae also to ossify from separate ossification centers in *Alligator*. Accordingly, dried skeletons of juvenile *Sphenodon* or *Alligator* may suggest the presence of free sacral or caudal ribs, absent in lizards.

In *Lacerta vivipara*, cartilaginous preformation of caudal transverse processes proceeds in an anteroposterior sequence, as does their ossification. In *Cyrtodactylus*, bony transverse processes were

added in an anteroposterior sequence without preformation in cartilage (Rieppel, 1992b). These observations support Patterson's (1977) distinction of exoskeleton versus endoskeleton: dermal bone (exoskeleton) has never been shown to be replaced by endochondral bone, but elements that are normally preformed in cartilage (endoskeleton) have been seen to ossify directly without preformation in cartilage in related taxa (membrane bones). "Whether membrane bones which are phylogenetic homologues of cartilage bones occur in tetrapods" was still considered an "open question" by Patterson (1977, p. 115). Posterior transverse processes in the caudal vertebrae of the gekkonid lizard *Cyrtodactylus* indicate the morphogenetic ability, in tetrapods, to replace endochondral bone by membrane bone.

Osteogenesis in the Appendicular Skeleton

OSTEOGENESIS AND PATTERNS OF REDUCTION IN GIRDLE ELEMENTS IN SQUAMATES—The sequence of ossification in the pectoral and pelvic girdles seems to be well defined: in the pectoral girdle, the clavicles ossify before the interclavicle, and ossification in the coracoid lags behind ossification in the scapula. In the pelvic girdle, the ilium is the first element to ossify, followed by the pubis and ischium. These sequences of ossification are mirrored in the sequence of reduction of girdle elements in a variety of lizards with reduced limbs (see below).

A number of surveys on limb reduction in lizards (Cope, 1892; Essex, 1927; Fürbringer, 1870; Kluge, 1976; Sewertzoff, 1931; Stokely, 1947; Siebenrock, 1895; Stephenson, 1962; Renous & Gasc, 1979) indicate that in pygopodids (Gekkota), scincids (Scincomorpha), and anguids (Angimorpha), the reduction of the dermal pectoral girdle always affects the interclavicle first, which may disappear while the clavicles still persist. Within the endochondral pectoral girdle, the loss of the pars coracoidea precedes that of the scapula (Fürbringer, 1870). Likewise, the ischium is the first element to be affected by reductions in the pelvic skeleton, followed by the pubis, while the ilium remains the most fully developed element. Fürbringer (1870) is the only author who has claimed that the pubis becomes reduced before the ischium. Males of the fossorial scincomorph lizard *Dibamus* retain a very rudimentary pubis, a small nodule of bone enclosing the obturator foramen (Greer, 1984, p. 137,

fig. 11). This rudimentary morphology corresponds almost perfectly to the earliest stages of endochondral ossification of the pubis in *Lacerta*!

Discussing the reduction of the pectoral girdle in squamates, Camp (1923 [1971], p. 353) was "struck by the marked resemblance of the extreme degenerative series to early embryonic stages in such elements. . . ." Perhaps, knowledge of the developmental pathway may successfully predict patterns of reduction (Alberch & Gale, 1985). The problem with this generalization in this instance is that it fails to distinguish endochondral from dermal skeletal components and does not take into account repatterning of the sequence of chondrification versus ossification within the endochondral component. That the interclavicle is reduced prior to the clavicle (Camp, 1923) is easily understood in view of their sequence of ossification, but how this should be related to the sequence of reduction or of ossification of the scapulocoracoid is unclear. In both *Sphenodon* (Howes & Swinerton, 1901) and *Lacerta* (Juhn, 1923, using histological techniques), the clavicles start ossification even before chondrification of the scapulocoracoid begins. This might explain why the clavicles persist while the interclavicle and scapulocoracoid have all disappeared in *Anniella*—but it does not explain why in scincomorphs the clavicles disappear before the scapulocoracoid (Camp, 1923, p. 369). These irregularities show that endochondral and dermal components have to be treated as potentially independent systems.

Similarly, it is unclear why the reduction of the pelvic girdle should mirror the sequence of its ossification, when reduction processes affect chondrogenesis of the respective elements. What little is known about reptilian pelvic development (Wiedersheim, 1889; Romer, 1942; Raynaud et al., 1975) indicates no clear temporal segregation of the origin of the pelvic elements. The obturator foramen is defined even before cartilage differentiates (Romer, 1942, p. 256), and this is the only indication of parallelism of chondrogenesis and osteogenesis, since the pubis first starts to ossify around the obturator foramen. Indeed, a reduction sequence may be expected to mirror the pattern of ossification only if no repatterning occurs in the sequence of osteogenesis as compared to chondrogenesis. Such, however, is the case in the limb skeleton.

THE OSSIFICATION OF LIMB ELEMENTS—Morphogenesis of tetrapod limb elements initially proceeds in a strictly proximodistal sequence. The

condensation of the stylopodial elements is followed by the differentiation of the zeugopodial elements, which in turn precedes the condensation of autopodial elements. Morphogenetic events in the reptile autopodium have most recently been reviewed by Burke and Alberch (1985) and Shubin and Alberch (1986; see also Müller & Alberch, 1990), who introduced the concept of the "primary axis" of limb development, referring to a predominance of the ulnar or fibular side of the limb during the process of condensation. From the ulna/fibula originate the ulnare and fibulare, respectively, as well as the intermedium. The ulnare/fibulare in turn give rise to dc4/dt4 and to one or several central elements. Distal carpal 4/distal tarsal 4 occupy a strategic position in the autopodium, as they represent the base of the digital arch: from them originate mc4/mt4 as well as dc3/dt3, which in turn gives rise to mc3/mt3 and dc2/dt2, and so on up to the first digit. Digit 5 originates as a *de novo* condensation and as such is not related to the digital arch. The corollary of that developmental scheme is that no radiale or tibiale segments from the radius or tibia, respectively, during the development of the reptile autopodium (Shubin & Alberch, 1986). This bears on the homology of the "radiale" and astragalus, but certain exceptions appear to exist. A radiale is formed in the carpus of *Alligator* (Müller & Alberch, 1990), while a "field of cartilage matrix" is observed to "connect the tips of the tibia and fibula condensation, forming a proximal arch of chondrogenic material" (Müller & Alberch, 1990, pp. 157–158). A radiale has also been claimed to form in the agamid lizard *Calotes* (Mathur & Goel, 1976; see also Raynaud, 1985, p. 79), and the cartilaginous precursors of the lizard astragalus still require closer analysis. Issues of homology will be dealt with in the next section. In this section, the focus is on two main aspects of Shubin and Alberch's model of limb morphogenesis, i.e., the primary axis and the digital arch, and how these relate to the process of ossification and limb rudimentation.

The sequence of ossification differs in important respects from that of limb chondrification. The proximodistal direction of limb differentiation is not recapitulated: stylopodial and zeugopodial elements start ossification almost simultaneously, to be followed by the metacarpals and metatarsals, followed in turn by the phalanges, while the carpal and tarsal elements ossify last. The primary axis of limb development is only partially preserved in the ossification of the forelimb, where the ulnare

ossifies before the “radiale” or intermedium, and dc4 is the first to ossify among the distal carpal elements and also ossifies prior to the centrale. In the hind limb, the astragalus is invariably the first element to start ossification, rather than the calcaneum (representing the fibulare). In *Lacerta vivipara*, dt4 always ossifies before dt3 (as in all other lizards so far investigated), but it may do so before or after the calcaneum has started to ossify. In the ossification of metacarpals and metatarsals, there is a predominance of the third digit in both manus and pes, whereas the primary axis runs through the fourth digit. The digital arch is only partially represented in the ossification sequence. Distal carpal 3/distal tarsal 3 invariably ossifies only after dc4/dt4, but in the manus, where more carpal elements are present, dc5 ossifies after dc2 and before dc1, and the ossification of the radiale, centrale, and pisiforme intervenes with the ossification of distal carpalia.

Differences in the sequence of chondrification as opposed to ossification may result from differences between two developmental control systems (Smith & Hall, 1990, p. 337–338). Shubin and Alberch (1986, p. 349) discuss paedomorphosis in relation to limb reduction in lizards, referring to Sewertzoff's (1931) study. They note that paedomorphosis is not in the bifurcation and segmentation sequences involved in limb morphogenesis but, rather, in the size of the (reduced) limb bud and the (reduced) number of cells it contains; Sewertzoff (1931, p. 661) concluded that “the sequence of reduction corresponds to the reversed sequence of embryonic formation of skeletal elements in forms with non-reduced limbs.” The consequence is that elements constituting the primary axis should be the last ones to disappear. Paedomorphosis affecting morphogenetic processes would result in the initial loss of digits 5 and 1, whereas digit 4 should be the last one to disappear. Paedomorphosis affecting the ossification of limb elements, however, would tend to preserve digit 3. Kluge (1976, p. 67) postulated the latter to be the case in pygopodids, but did not relate this conclusion to a consideration of developmental mechanisms. Sewertzoff (1931), on the other hand, presented a convincing argument that the fourth digit is the last one to disappear in squamates. The sequence of digital reduction is $1 > 5 > 2 > 3 > 4$, which matches the chondrification sequence within the digital arch better (note that digit 5 is a *de novo* condensation not connected to the digital arch) than the ossification sequence of metatarsals (which would predict digit 5 to become reduced

first and digit 3 to be the last one to disappear). A pattern of reduction similar to the one discussed by Sewertzoff (1931) is described by Greer (1990a,b, figs. 82–83) for the scincid genus *Lerista*, the only difference being the relatively late disappearance of a rudimentary mt5 (not part of the digital arch). (Steiner and Anders [1946] disagreed with Sewertzoff's [1931] interpretation of *Chalcides tridactylus* and believed that it is not the first and fifth digit that become reduced in the manus, but the fourth and fifth. This conclusion was based on a morphological comparison implying the homology of dc1 with the epiphysis on the proximal head of mc1, and the absence of a hooked morphology of the rudimentary lateral metatarsal, which they accordingly interpreted as mt4. The homology of free carpal [or tarsal] elements with epiphyses is here rejected [see below], and absence of hooking in mt5 is the result of truncated development.)

Whereas the reduction of digits mirrors the primary axis of limb development and its importance in morphogenesis, this does not seem to be true for carpal and tarsal elements. Essex (1927) documented a high degree of variability of the reduction pattern in the carpus of *Chamaesaura anguina*, although the semidiagrammatic style of his figures renders their interpretation difficult. A morphocline of carpal reduction, composed of six species of *Lerista*, was figured by Greer (1990a), indicating a sequence of reduction beginning with $dc1 > dc5 > dc2$, centrale $> dc3$; at the same time, digits are reduced, and the ossified epiphyses apparently fail to fuse to the distal ends of the tibia and fibula. The latter point indicates that limb reduction does affect ossification processes, and indeed the ossification sequence in the carpus of *Lacerta vivipara* is $dc4 > dc3 > centrale > dc2 > dc5 > dc1$ (ossification of the radiale and pisiforme intervenes with that sequence at variable times). The reduction pattern in the carpus of *Lerista* therefore mirrors the ossification sequence in the carpus of *Lacerta* to a greater degree than the chondrification sequence described by Shubin and Alberch (1986): the latter would predict an earlier ossification and a later loss of the centrale (although Sewertzoff, 1931, fig. 32, showed the chondrification of the centrale only after the formation of dc4 and dc3 in *Chalcides chalcides*). That the sequence of reduction of carpal elements mirrors the reversed sequence of ossification is also indicated by Sewertzoff's (1931, p. 637, fig. 13) description of the carpus of *Chalcides tridactylus*, where dc1, dc2, and dc5 have been lost entirely,

and the centrale remains cartilaginous whereas dc3 and dc4 ossify (as well as the "radiale" and ulnare): failure of ossification appears to precede complete absence in that case.

Similar conclusions pertain to the reduction of tarsal elements. Distal tarsal 3 is always lost prior to dt4, corresponding both to the reversed sequence of their formation in the digital arch and to the sequence of their ossification. In the proximal tarsus, however, the fibulare (precursor of the ossified calcaneum) develops before other rudiments that fuse into the astragalus, whereas the astragalus ossifies first and appears to be the last element lost (Essex, 1927; Sewertzoff, 1931; Greer, 1990a, fig. 83). The first appearance of the astragalus is distal to the spatium interosseum between the tibia and fibula, which is also the position of the single and last tarsal element retained in taxa with extensive limb reduction (see Essex, 1927; Sewertzoff, 1931; and Greer, 1990a, fig. 83, for examples).

The limited evidence available at this time allows us to distinguish two types of skeletal reduction, one relating to morphogenesis of cartilaginous precursors, the other relating to patterns of ossification, the two not necessarily being congruent. The difference is of importance in the interpretation of fossil skeletons, in which the absence of an element may be due either to failure of its formation or to lack of ossification.

Ontogenetic Repatterning

Following the developmental pattern outlined by Shubin and Alberch (1986), a true radiale and tibiale, segmenting from the radius or tibia, respectively, do not form in reptiles: exceptions are *Alligator* (Müller & Alberch, 1990) and perhaps lizards (Mathur & Goel, 1976). The element normally called the radiale in reptiles would form, instead, by the fusion of the intermedium with one or more centralia (Shubin & Alberch, 1986). Looking at the precursor of the radiale in *Lacerta*, it is indeed apparent that it consists of an expanded head in an intermedium position, from where it extends laterally to the space distal to the radius. Ossification begins in the expanded lateral head, close to the ulnar side of the cartilage, and only later spreads medially. MBS 16487 shows two centers of mineralization in the cartilaginous precursor of the radiale: a large one in the expanded lateral head, and a small one medial to it and distal to the radius. These two centers might be thought

of as representing the original intermedium, fusing with an originally separate centrale. Haines (1969, p. 107, fig. 25) reports two centers—a large center of ossification on the lateral side and a smaller center of calcification on the medial side—in the "radiale" of a juvenile specimen of *Varanus niloticus*, but he compared the center of calcification to an epiphysis on the "radiale." The fusion of a large and well-defined lateral ossification center with a separate and small medial calcification/ossification center within the cartilaginous precursor of the radiale was also observed in the varanoid lizard *Lanthanotus* and in four juvenile *Varanus* (*bengalensis*, *exanthematicus*, *griseus*, and *salvator*) (Rieppel, 1992a), and a suture is shown in the fully ossified radiale of *Varanus bengalensis* by Renous-Lécuru (1973, fig. 33).

The interpretation of the two centers of mineralization within the cartilaginous precursor of the radiale as the original intermedium and centrale raises a number of questions. As the center distal to the radius is an epiphyseal calcification (Haines, 1969), the centrale, a genuine carpal element, would be homologized with an epiphysis. However, a separate epiphyseal calcification was also observed on the ulnare of *Lanthanotus* and of two juvenile *Varanus* (*exanthematicus* and *griseus*) (Rieppel, 1992a), and Mathur and Goel (1976) described epiphyses on both the radiale and ulnare of the agamid *Calotes*. There is no reason why an epiphyseal center on the radiale should be homologized with a centrale, whereas no homology with originally separate carpal elements is sought for epiphyseal calcifications on the ulnare, or on distal carpals (Dollo, 1884; Mathur & Goel, 1976). It seems highly questionable to homologize originally separate carpal elements with epiphyseal centers of calcification and ossification, because such conjectures of homology generally fail the test of conjunction (Patterson, 1982).

The situation is further complicated by the presence, in *Lacerta*, of a small cartilaginous nodule that lies between the distal ends of the radius and ulna and that ossifies separately, although late, in ontogeny. If this element, first recognized by Born (1876), indeed represents the intermedium, the large lateral ossification center in the expanded head of the cartilaginous precursor of the radiale cannot also be interpreted as such. A small, separate intermedium between the distal ends of the radius and ulna is of highly variable occurrence throughout lizards (Renous-Lécuru, 1973), and it may be absent in the cartilage stage (*Cyrtodactylus*: Rieppel, 1992b; *Lanthanotus*: Rieppel, 1992a),

which would not seem possible given Shubin and Alberch's (1986) model of morphogenesis. Several possible conclusions result: the intermedium may be incorporated in the radius (Shubin & Alberch, 1986), and the "intermedium" of Born (1876) must be a neomorph. Alternatively, the intermedium of Born (1876) is the true intermedium, frequently absent in lizards, and lizards form a true radiale. The situation must remain unresolved until patterns of connectivity in the morphogenesis of the lizard carpus are more completely understood.

Problems similar to those discussed in relation to the radiale also arise in the interpretation of the astragalus, claimed to incorporate the amphibian tibiale, intermedium, and proximal centrale (Peabody, 1951; Huxley, 1872, p. 178, believed the astragalus to include the tibiale and intermedium; Schaeffer, 1941, believed a true tibiale to be absent in reptiles). Whatever the homology and number of cartilaginous precursors of the proximal tarsal bones, they all lose their identity as they fuse into a single proximal cartilage, the tarsale proximale of Sewertzoff (1908). Within that cartilage, both the astragalus and calcaneum ossify from a single center, the astragalus first appearing in an intermedium position. Romer (1956, p. 393) considered this a "secondary simplification of the developmental process," but in a footnote to page 393, he mentioned the possibility of fusion of the astragalus with additional ossification centers, which he identified as additional "adjacent" tarsal elements with no bearing on "the question of primary formation of the bone." In fact, these additional "elements" again represent epiphyseal centers that may form both on the astragalus and on the calcaneum (see Rieppel, 1992c, for further details). Again, the option to homologize epiphyseal centers with original tarsal elements seems inapplicable, nor does it seem possible to equate the astragalar ossification with specific cartilaginous precursors.

Homologies of Epiphyseal Centers

Epiphyses of lizards do not start calcification and/or ossification until after birth or hatching (Moodie, 1908, p. 445). Although recognized as a lepidosaur synapomorphy (Gauthier et al., 1988), there is to the present date no systematic account of the appearance and distribution of epiphyses in any lizard species (Haines, 1969, p. 104), the most complete account still being that of Dollo (1884). In lizards, epiphyses typically calcify before being

replaced by endochondral bone (Haines, 1969). De Ricqlès (1976, pp. 137–138) found that ossification of the epiphyses proceeds from the metaphysis in *Sphenodon*, whereas secondary centers of ossification in the epiphyses of squamates are usually conspicuous. Much remains to be learned with respect to epiphyseal ossification in lepidosaurs.

Early authors such as Gegenbaur (1864), Born (1876, 1880), and Baur (1885) homologized originally separate carpal elements with epiphyseal calcification and ossification centers, which eventually fuse with adjacent bones. Similar hypotheses are put forward in the modern literature. Based on topological relations, Carroll (1977, p. 374) concluded that the element usually identified as dc1 in lizards (*sensu* Renous-Lécuru, 1973) corresponds to the medial centrale, whereas distal centrale 1 is represented by the epiphysis on the proximal head of the first metacarpal (see also Steiner, 1922, and Steiner & Anders, 1946, who proposed the same homology). This character is thought to be diagnostic for the Lepidosauria (Gauthier et al., 1988, p. 57). In support of his argument, Carroll (1977) quoted Haines (1969, p. 104), who quoted older authors indicating that only the distal heads of the metacarpals and the proximal heads of the phalanges show growth and separate epiphyseal centers in lizards, except for mc1 in *Varanus griseus*, which also had an epiphyseal center at its base (Fuchs, 1908, p. 356). In *Lacerta vivipara*, the phalanges bear distinct and separate epiphyseal centers at the proximal end only, but the metacarpals and metatarsals all bear separate epiphyseal centers on both proximal and distal heads. The same is true for the gekkonid genus *Cyrtodactylus* (Rieppel, 1992b) as well as for juveniles of the varanids *Lanthanotus* and *Varanus* (Rieppel, 1992a) and for all other lizards investigated so far. Heidsieck (1928, pp. 425–426, 430) reported exceptions such as the absence of separate epiphyseal centers on the proximal and distal heads of the metacarpals in *Draco fimbriatus* and *Draco* sp., a claim that corresponds to Moodie's (1908, p. 457) observations, but that could not be confirmed in a series of cleared and stained specimens of *Draco melanopogon*. There is, therefore, no reason why the epiphysis on the proximal head of mc1 should be homologous to dc1, whereas those on the other metacarpals are considered to be just what they are—separate epiphyseal centers.

The same problem pertains to the interpretation of the hooked fifth metatarsal, diagnostic of lepi-

dosaurs. Since the seminal paper by Goodrich (1916; see also Robinson, 1975), the hooked fifth metatarsal has been an important character for reptile classification (Huxley, 1872, p. 179; Goodrich, 1942; Benton, 1985; Evans, 1988; Gauthier et al., 1988). Yet no attention has been paid in recent times to its ontogenetic development. The controversy as to whether or not the expanded proximal head of the fifth metatarsal incorporates a dt5 (Huxley, 1872, p. 192; Goodrich, 1916; Dollo, 1929; Robinson, 1975) has been resolved with reference to older literature (e.g., Sewertzoff, 1908), which was misinterpreted at least to some degree. Gegenbaur (1864) and Baur (1885) treated epiphyseal ossification centers as individual elements and claimed that the proximal head of mt5 incorporates the fifth distal tarsal. Such is not corroborated by the pattern of ossification of mt5, however.

In all lizards investigated, mt5 is severely delayed in ossification. During early stages of development, it is represented by a simple, slender, and slightly curved rod of cartilage, the proximal end being somewhat deflected medially. Further growth results in an expansion of the proximal head, which results in a distinct medial "notch" marking the angulation between the medially expanded proximal head and the slender shaft of the element. The proximal head of mt4 comes to lie in this angulation where the medial plantar tubercle starts to form, again as a result of cartilage growth (for a detailed description of the fully formed hooked fifth metatarsal, and the terminology involved, see Robinson, 1975). The dorsoventral flexion of the element, characteristic of lepidosaurs, becomes apparent as perichondral ossification begins in the medial angulation and at the base of the medial plantar tubercle. The latter continues to grow as the lateral plantar tubercle differentiates in cartilage and perichondral ossification spreads around the midshaft area. Again it is the midportion of the diaphysis that first undergoes endochondral ossification, leaving the large proximal head and the distal epiphysis as well as the tips of the medial and plantar tubercles unossified. The lateral process is not yet distinctly set off from the cartilaginous proximal head.

As development progresses, the diaphyseal ossification invades the base of the expanded proximal head, and epiphyses will eventually start to calcify and ossify on both the proximal and distal heads of mt5. However, two separate epiphyseal centers calcify on the proximal head. The first to appear is on the medial aspect of the proximal

head, at the articulation with the proximal head of mt4 and with dt4. A second, smaller epiphysis caps the outer process, adding to its distinctiveness. In summary, no originally separate cartilaginous precursor of dt5 has ever been observed to fuse with the *anlage* of mt5. Any conjecture of homology of dt5 with epiphyseal centers on the proximal head of mt5 must specify why any one of the two centers should represent dt5 as opposed to the other and what the serial homology is of the proximal epiphyses of the other metatarsals. (Steiner and Anders [1946] believed that rudimentation of the limbs in *Chalcides tridactylus* results in a secondary separation of dt2 from the proximal head of mt2. Their digital count seems erroneous, however. They identify mt4 on the basis of absence of the hooked morphology characteristic of mt5, but in view of the rudimentary nature of the element, and the account of the development of mt5 given above, this is easily explained as a result of truncated development. On a revised digital count, their mt2 becomes the mt3.)

Summary: The Concept of Skeletal Paedomorphosis

The concept of skeletal paedomorphosis (*néoténie squelettique*) was first introduced by de Ricqlès in 1975 (see also his more recent review of 1989), who brought into focus the high degree of regularity and convergence of reduced (globally and/or locally "truncated") ossification in aquatic tetrapods. The regularity of the phenomenon suggests underlying causes at the genetic, endocrinal, and "epigenetic" (environmental) levels. Skeletal reductions play an important role in the morphology of fossil marine reptiles from the Middle Triassic (Rieppel, 1987a, 1989a,b). Reduction is most conspicuous in the carpus and tarsus. The understanding of fossil morphologies subject to skeletal reduction would be greatly improved if it could be shown that patterns of reduction mirror developmental pathways in a reversed sense (Riedl, 1978). Knowledge of ontogeny could then be used in the prediction of (perhaps clade-specific) patterns of reduction.

The comparison of ossification patterns with reduction patterns requires the distinction of endochondral versus dermal (*sensu* Patterson, 1977) compartments of the skeleton, which seem to be developmentally decoupled to some degree (see also Smith & Hall, 1990). The preceding discus-

sion indicates, for example, that the pattern of digital reduction mirrors the importance of the primary axis in limb morphogenesis (Shubin & Alberch, 1986), whereas patterns of reduction in carpus and tarsus mirror patterns of ossification. Since patterns of ossification do not mirror patterns of chondrification in every respect, different fossil skeletal morphologies may result, depending on which aspect of development is affected by paedomorphosis. Accordingly, two types of skeletal paedomorphosis must be distinguished. Paedomorphosis may truncate, locally or globally, morphogenetic processes, resulting in reduced structures caused, in the limb, mainly by the size of the limb buds and the corresponding numbers of cells (Sewertzoff, 1931; Raynaud, 1985; Shubin & Alberch, 1986). Alternatively, paedomorphosis may affect the ossification process within skeletal structures preformed in cartilage, as is the case in *Chalcides tridactylus* (see above) and as must also have been the case in fossil marine reptiles (Rieppel, 1987a, 1989a,b). Therefore, a single tarsal bone in an intermedium position in a reduced reptile limb corresponds not to the intermedium but to an early stage of ossification of the astragalus, the first tarsal element to ossify. Although the morphogenetic rules described by Shubin and Alberch (1986) require, at some stage of morphogenesis, the presence of a fibulare, the latter may not ossify and hence may appear to be absent in fossils.

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